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## ADAPTATION AND THE PROBLEM OF "ORGANIC PURPOSEFULNESS." II

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### IV. THE PRINCIPLE OF TRIAL AND ERROR IN RELATION TO REGULATIVE PHENOMENA<sup>14</sup>

Driesch and some other vitalists draw their most effective ammunition from the phenomena of experimental embryology and regeneration. How is it that a fragment of a developing organism—any fragment, within certain limits—can produce the whole? How is it that various perversions of the normal course of development do not prevent the attainment of the normal end? How is it that certain adult organs, *e. g.*, the lens of the eye of a triton, when removed by a highly "unnatural" operation, is nevertheless restored, and restored by a process quite different from that in which it is normally produced in embryonic development?

At the outset we must make two admissions: (1) that these processes can not be the result of a mechanism specifically adapted in advance to meet these particular exigencies, and (2) that they can not be satisfactorily explained by assuming any preformation of the parts which are restored. The former supposition is to be re-

<sup>14</sup> The "trial and error" principle has of late years come into the foreground of biological discussion, largely through the writings of Jennings. It was, so far as I know, first clearly proposed (though not so named) by Spencer (*Principles of Psychology*, Vol. I, pp. 544-545) to account for the origin of adaptive responses to stimuli, and was later developed by Bain. There are important points of agreement between the views of these writers and some of those set forth independently by Roux in his classic essay, "Der Kampf der Theile im Organismus" (1881). More recently, Baldwin (*Mental Development*, 1898, Chapter VII; *Development and Evolution*, 1902, pp. 108-115) has further elaborated the same fundamental idea as that of Spencer and Bain in his theory of "functional selection." Various animal psychologists (*e.g.*, Lloyd Morgan and Thorndike) have also laid stress on this principle.

jected on account of the unusual and artificial character of the operations, which could never have been provided for by natural selection, nor, so far as we can see, by any other recognized principle of evolution. The latter supposition is sufficiently disposed of by Driesch's analysis (section III) and need not be considered here.

Driesch admits that a physico-chemical machine "might very well be the motive force of organogenesis in general, if only normal, that is to say, if only undisturbed development existed, and if a taking away of parts of our systems led to fragmental development" (II, 139). If, therefore, we can explain these critical cases without invoking any principles beyond those believed to be operative in normal life-history, we have disposed of this line of argument.

In an earlier section of this paper I took the ground that an adaptive or "purposive" response by the organism, if not guided by past individual or racial experience, must be the result of experimentation. I avoided intentionally at the time any consideration of those cases of regeneration and form regulation in which the emergency was totally new, and therefore foreign to the experience of the organism or its ancestors. Here a specially evolved mechanism could hardly be invoked. I suggested, however, that the principle of "trial and error" could be applied to these cases. This suggestion was, of course, not new. Such an extension of this conception had already been made by Jennings,<sup>15</sup> though it is rather surprising to note that he has given it little further consideration in his recent discussions of vitalism. For, to my mind, an explanation involving this principle, seems the only alternative at present to a vitalistic one, or, better stated, it seems to me the only alternative to an abandonment of the search for a scientific explanation.

According to the trial and error principle, as applied to the movements of a lower animal, "behavior that results in interference with the normal metabolic processes

<sup>15</sup> "Behavior of the Lower Organisms" (1906), Chapter XXI.

is changed, the movement being reversed, while behavior that does not result in interference or that favors the metabolic processes is continued.”<sup>16</sup> The primary “avoiding reaction,” in the presence of an unfavorable stimulus, is, of course, comparable with a simple reflex. Its ordinary effect is to remove the organism from the noxious influence. When progressive movements are resumed, they occur at random, so far as their direction is concerned, and they may or may not take the organism into favorable surroundings. If they chance so to do, they are continued indefinitely. If not, the reversal of movement occurs as before. Thus while, to the uncritical observer, the organism seems to “seek out” the optimum environment, it really reaches this through a series of accidents. This is as true of a cat, releasing itself from an experimental trap, as it is of a paramœcium escaping from a harmful to an optimum water temperature. In the case of the cat we may be tolerably sure that the animal experiences a feeling of discomfort until the means of escape is discovered, and we find it convenient, if not inevitable, to say that her restless movements are the *result* of this feeling. In the case of the infusorian, we are much less sure of the conscious element, though its introduction is permissible as an act of philosophic faith. In theory, most scientists are probably psychophysical parallelists, but in practise it seems necessary at times to use the language of interactionism. In discussing the voluntary movements of a higher animal, any other course would seem pedantic. But in discussing the simple behavior of a lower organism, such language is commonly branded as “anthropomorphic.” Nevertheless, I believe that its employment even here is sometimes useful in forcing us to keep in view the essential unity of animal life. No protest is raised by the physiologist when thoroughly *protozoomorphic* language is applied to a vertebrate. Why then should “anthropomorphic” terminology so shock us in describing the be-

<sup>16</sup> Jennings, *op. cit.*, p. 39.

havior of a *Paramaecium*? Each is the extension of an article of philosophic faith far beyond the realm of experience. But this is no essential part of our present argument. Let us consider whether the trial and error principle may not be applicable to other phenomena than the bodily movements of animals.

Jennings asks :

Is it possible that interference with the physiological processes may induce changes in other activities,—in chemical processes, in growth, and the like,—and that one of these activities is selected, as in behavior, through the fact that it relieves the interference that caused the change? . . . It is evident, then, that the organism has presented to it, by the condition just sketched, unlimited possibilities for the selection of different chemical processes. The body is a great mass of the most varied chemicals, and in this mass thousands of chemical processes, in every direction,—all those indeed that are possible,—are occurring at all times. There is then no difficulty as to the sufficiency of the material presented for selection, if some means may be found for selecting it (*op. cit.*, p. 346).

Looking for evidence that such a process of selection does actually occur in physiological regulation, Jennings cites the experiments of Pawlow, in which the latter habituated dogs to various kinds of foods and noted the effects upon the digestive juices. In these experiments the adaptive changes in the activities of the digestive glands, fitting the digestive juices to the food taken, do not occur at once and completely under a given diet, but are brought about gradually. . . . This slow adaptation is, of course, what should be expected if the process occurs in anything like the manner we have sketched (p. 347).

Jennings concedes :

It is perhaps more difficult to apply the method of regulation above set forth to processes of growth and regeneration. Yet there is no logical difficulty in its way. The only question would be that of fact, whether the varied growth processes necessarily do, primitively, occur under conditions that interfere with the physiological processes. When a wound is made or an organ removed, is the growth process which follows always of a certain stereotyped character, or are there variations? It is well known, of course, that the latter is the case. . . . Removal of an organ is known to produce great disturbances of most of the processes in the organism and among others in the process of growth. . . . Some of these relieve the disturbance; the variation then ceases and these processes are continued (p. 348).

A line of argument which has points of similarity to the foregoing has been independently developed by Holmes.<sup>17</sup> He believes:

The harmonious functioning of an organism is mainly secured by a system of automatically acting checks which we may conceive to act in manner more or less remotely analogous to the governor of a steam-engine or the forces which regulate the motions of the planets. . . . In these cases deviation from the normal is the cause which automatically sets up activities by which the normal is regained.

So, too,

the self-regulation of organisms may . . . be in a measure understood if we assume that their parts stand in a relation of mutual dependence such that the undue growth or functioning of any part is held in check by the reactions thus brought about by other, and especially the contiguous structures. If we suppose that the various cells constituting the body have each a different kind of metabolism, and that the products of each cell are in some way utilized by the neighboring cells, so that each derives an advantage from the particular association in which it occurs, we may understand, in a measure, how this checking may be brought about.

And here an analogy is pointed out with the relations which obtain in "symbiotic" communities, such as those composed of animal cells and certain unicellular algæ.

The conception here developed is in some respects an extension of Roux's intra-selection hypothesis, though Holmes rejects the notion of a "struggle of the parts." This conception, which derives strong support from recent discoveries respecting "hormones," gives a certain measure of concreteness to that rather vague expression, "the organism as a whole." For, despite the many known instances of local autonomy, we can not doubt that the organism does in a high degree act as a whole. But this "wholeness" may not be an irresolvable fact, as has sometimes been assumed. It may be possible to conceive it in terms of chemical and structural integration.<sup>17a</sup>

This hypothesis, as applied to form regulation, would

<sup>17</sup> *Archiv für Entwicklungsmechanik*, 1904.

<sup>17a</sup> To me, such a viewpoint seems quite reconcilable with the "organismal" conception of Ritter, though Professor Ritter himself (*The Unity of the Organism*, Vol. I, p. 183) has gone to considerable pains to show the fallacy of Holmes's position.

seem to be closely related to that of Jennings, and indeed Jennings himself views it in this light. It is difficult to gather, however, to what extent Holmes has in mind the principle of "trial and error." His comparison of regeneration with functional hypertrophy does not seem compatible with this principle. "Remove one of a pair of organs," he says, "and its fellow increases in size. Remove a part of one of these organs and the remaining portion grows, forms new tissue, and regenerates the missing part." Furthermore, he believes that these phenomena may be analogous with some of those described under the name of "chemical equilibrium."

The decomposition of compounds in solution proceeds until there is a definite relation established between the amounts of the old compounds and the new. If the chemical equilibrium thus established is disturbed by the removal of one of these compounds more of that compound will be produced; and the more rapidly the compound is removed, the more rapidly it is formed.

Such an "automatic" restoration of equilibrium as this might seem to be a radically different thing from trial and error. The process by which it is attained would appear to be direct and unhesitating. Holmes says that the solar system, no less than the organism, is a "self-regulating mechanism." Now, in the former, the balance of its opposing forces is effected "automatically" in the sense that any deviation in the movement of one of the parts would result inevitably in a compensating deviation in the others. Is the restoration of an organism to its norm of this direct and automatic type? Are such processes as tend to compensate a disturbance in the normal functioning of an organism the direct and exclusive result of the disturbance itself, or does this disturbance evoke a variety of responses of which the suitable response may finally happen to be one? The first of these alternatives may be admitted as probable in the case of such disturbing factors as have been frequently experienced in the past. But how does it happen that certain cells of the iris of a newt become stimulated to division by the removal of the lens? And why should

their metabolism become so affected that they give rise to lens tissue, instead of to iris tissue? Can we believe that the iris cells proceeded unfalteringly to this end as a result of the operation?

The discussion after all hinges upon the word "unfalteringly," and this term has been applied to processes which are beyond the possibility of direct observation. If we grant that a disturbance of growth equilibrium was what led to the reparative processes, and that equilibrium was in the end restored, it does not seem difficult to admit that each minutest step in the direction of restoring this equilibrium was selected from a medley of random reactions. Indeed, Holmes suggests that cells which develop in the direction of the missing part receive those advantages which the symbiotic relation afforded the cells whose place they take. Differentiation in any other direction deprives them of these advantages and subjects them to other unfavorable conditions.

Nor need it be assumed that these responses are wholly random. Although it is incredible that each type of possible injury has been provided for in advance by a specific mechanism, it seems more than possible that certain reactions have been acquired which are of service in *any* emergency—a sort of "first aid to the injured," as we might say. After these preliminary steps of a general character—which are, as a matter of fact, the common precursors of regeneration<sup>18</sup>—the more special processes may be supposed to proceed in a tentative fashion.

All that is meant by "growth equilibrium," in this discussion, is such a normal state of metabolic balance that the growth of each part is checked through its organic relations with the rest. Attainment of this goal would bring the organism into a condition of "no stimulation," like that of the protozoan which has escaped from an unfavorable environment.

Since we commonly are able to observe only the final outcome of such a process, and overlook the minute steps

<sup>18</sup> These steps are frequently retrogressive ones and include the loss of specialized structures.

by which it comes to pass, we are wont to believe that the reparative activities move directly toward the end which we observe to be ultimately attained. Thus Driesch tells us that

the process of restitution, perfect the very first time it occurs, . . . is the classical instance against this new sort of contingency. . . . Here we see with our own eyes that the organism can do more than simply perpetuate variations which have occurred at random.

What we see with our own eyes, as I have already said, is only a series of visible stages in the process of restitution. We *do not see* the inmost morphogenetic processes, physical and chemical, by which this end is attained.

Perhaps it may seem that the foregoing explanation merely resorts to the familiar expedient of throwing our difficulties back into an invisible realm where they are safely beyond the reach of scientific investigation. I would say first of all that even this type of explanation, which at least speaks in the language of known facts, is preferable to one which frankly abandons scientific principles altogether. And secondly, I would point out once more the possibility that this hypothesis is one which may in reality be put to experimental test. For any indication of a profiting by "experience," *i. e.*, of a shortening of the time required to effect a given regulative response, would harmonize well with the hypothesis that the response was at first effected through tentative steps. Indeed, such evidence, even now, is not wholly lacking.

It may be well to remind ourselves at this point that the perfect regeneration of missing parts, or the complete reconstruction of a mutilated embryo is after all an exceptional phenomenon. Many animals almost entirely lack the power of regeneration, while most injured eggs either die or give rise to abnormal embryos. These facts harmonize best with the view that regenerative processes are causally produced in the same sense as inorganic phenomena, and that they are not determined, in any direct way, by needs or ends to be realized. The forma-

tion of misplaced, supernumerary and other useless structures, and the occurrence of anaphylaxis, instead of immunization, certainly do not argue for the existence of a "primary teleology" in nature, though, of course, they do not wholly refute it.

On the other hand, the occurrence of these non-adaptive responses to growth stimuli is no more inconsistent with an intra-selection hypothesis, such as that here advocated, than is the occurrence of multitudes of non-adaptive structures or colors in nature inconsistent with the theory of natural selection. There must be rigid limitations to the operation of both processes. The task which I have undertaken here is not to explain structures and function in general, but the more modest one of trying to explain why certain among these are directed toward the conservation of the individual or the species. If various other vital phenomena are found to be non-adaptive, our difficulties ought not to be increased.

There are cases, it is true, in which some simple physical factor, such as gravity, or the plane of section, may determine whether the actual missing part is restored or a misplaced organ is the result. It certainly seems arbitrary to offer fundamentally different explanations in the two cases. Now, I have nowhere made the contention that the processes involved in regeneration are wholly random, in the sense of being unrelated to one another and to the past history of the individual. In normal development the processes are doubtless so concatenated that growth and differentiation proceed in a direct way with little or no "lost motion." And every detached portion of such an organism must receive its share of this established developmental machinery. The tendency to reconstruct the whole, to attain the normal specific form, is therefore opposed by another set of tendencies, urging it to develop as if it were still part of the undivided organism. As is well known, the outcome of this conflict of forces varies, depending upon the species of animal and the time of operation. We may have

either total or fractional development as a result. It does not seem unlikely, therefore, that in every case of regeneration the control of the "organism as a whole" is opposed, more or less successfully, by the specific growth tendencies of the various cells and tissues from which restitution proceeds. These might, in consequence, bring about the "autonomous" production of a wholly misplaced part.<sup>19</sup> Thus the phenomena of "heteromorphosis" should seem to offer no insuperable obstacle to the views herein set forth.

Applied to the ordinary phenomena of regeneration, say to the restoration of an amputated limb, or even the lens of an eye, this hypothesis of achievement through experimentation would seem to make no impossible demands upon our imagination. We need only suppose that the absence of the missing part serves as a stimulus to varied and undirected metabolic activities, that such of these as serve to restore the normal condition tend to be continued and that growth equilibrium (absence of stimulus to growth) is not normally attained until the missing part is restored. The case would seem to be not very different from that of an animal finding its way out of an unfavorable environment. In both instances we may suppose the organism to be in a condition of "unrest" until the end is achieved. This condition may or may not be conceived in psychical terms. If so conceived, the notion would be philosophically legitimate, though scientifically unnecessary.<sup>20</sup>

When, however, we consider Driesch's crucial case of the development of an entire organism from an embryonic fragment, the matter is admittedly far less conceivable. For this fragment has retained nearly or quite the same potentialities as the entire egg or embryo, in that its career of multiplication and growth is brought

<sup>19</sup> This explanation of heteromorphosis is, I think, quite in harmony with that offered by Holmes (*op. cit.*, pp. 302-303).

<sup>20</sup> Cf. Baldwin's statement ("Mental Development," p. 177): "*the life-history of organisms involves from the start the presence of the organic analogue of the hedonic consciousness.*"

to a close only through the attainment of the form which is typical for the species in question. Why should this ultimate condition of equilibrium be the same whether we start from an isolated blastomere, an irregular fragment of a blastula or a normal egg? Does it not seem as if the only constant feature in this case were the end itself? In considering the behavior of a protozoan, the stimuli may vary and the method of escape may vary, but the organism itself is the same. The "equi-finality" of the result—to use an expression of Driesch's—may be attributed to this fact that we are dealing with the same physico-chemical system, and one of the self-regulating type. But what of our various embryonic fragments? Are they not obviously different physico-chemical systems?

Now, after all, the difference between this case and that of a regenerating limb or lens appears to me to be only one of degree. The distinctions relate (1) to the stage in development at which the injury is inflicted, and (2) to the proportional part of the organism which is left to reconstruct the remainder.

1. As regards the first point, we must suppose that at each stage of ontogeny such a state of physiological balance is normally maintained as is appropriate to that particular stage. That the multiplication and differentiation of certain cells is profoundly influenced by the presence or absence of other cells is one of the assured results of experimental embryology. One need only cite the difference between the development undergone by an amphibian blastomere which is totally detached at the two-celled stage, and that of the blastomere whose partner has been injured by a needle-prick and left in position.

Thus we have as much right to assume for the blastula as for the adult animal that any disturbance of metabolic balance will be followed by varied responses, some of which will tend to restore the balance normal to that period. The fact that these responses are known to differ radically, following the same type of operation,

and that the result is often a very imperfect reconstruction of the whole, lends support to the view that the cells of the injured embryo "feel their way"—so to speak—back into a condition of mutual equilibrium. In some cases this equilibrium appears to be of a simple physical sort, as for instance, that which is brought about by the folding together of the edges of a blastula fragment so as to reconstruct the spherical form. But in most cases the factors are doubtless vastly more complex.

Once the reconstruction of the normal embryonic form is attained, the difficulties in understanding the further stages of ontogeny are no greater than we meet with in the case of an uninjured embryo—that is, unless we are encumbered by a preformation theory of development.

2. As regards the second point above raised, there is theoretically no greater difficulty in understanding how one tenth of an organism may restore the remaining nine tenths than in understanding how the nine tenths may restore the one tenth. As a matter of fact, in dealing with certain organisms, the size or shape of the piece, or the region of the body from which it is taken count for little in the outcome. But they do count for something, and that something is significant. It has been found in some cases, for example, that there are lower limits to the side of the pieces which may carry out development or regeneration. And in other cases, the position of the plane of section may determine whether a useful structure is formed or one which is wholly useless.

But whether or not the size or shape of the fragment count for anything in the reparation of a given organism, we find that the *species* from which it is taken counts for everything. There must, therefore, be something that is common to all detached portions of an organism which are capable of reconstructing the same whole. The portion in question may be an asexual spore or a fertilized egg, or it may be an isolated blastomere or other artificially detached fragment of either an embryo or adult organism. What is this greatest common divisor? Is it a unit of structure or is it a chemical substance?

There would seem to be no third possibility, as long as we keep within the bounds of scientific explanation. But a unit of structure may none the less be itself a chemical individual. Modern speculative physics refers all qualitative differences in the last resort to differences of structure, even in the case of the elements. And it has been suggested that the various specific protoplasms, which are responsible for the slightly different metabolic products of different species, owe their differences to stereoisomers, *i. e.*, substances which agree quantitatively in their composition, but whose enormously complex molecules differ as the result of some slight transposition of atoms or radicals.<sup>21</sup>

To the majority of present-day geneticists there is doubtless a ready answer to the question: what is this something that is common to all detached portions of an organism which are capable of reconstructing the same whole? It is likely that to most of them a completely satisfactory answer would be: *the cell nucleus*. Thus Jennings,<sup>21a</sup> in discussing specifically certain of the questions raised by Driesch, assures us that "the recent study of genetics has shown that this [the chromosomal] apparatus is the system on which the peculiarities of development mainly depend. This system is not equi-potential; the fate of its parts is not a function of their position; it has a complex structure with a corresponding complexity of action; altering any of its parts alters correspondingly the action of the system; irregular removal or disarrangement of the parts destroys the action."

Whether or not this aggregate chromatin matter of the nucleus constitutes the *minimum divisible* of the organism, as recent students of heredity are disposed to believe, is still quite undecided. For protozoa we are definitely able to state that this is not true. Experiments in regen-

<sup>21</sup> Reichert, *Science*, November 6, 1914. This article contains much interesting evidence for the chemical distinctness of genera and species, and even of individual organisms.

<sup>21a</sup> *Philosophical Review*, Nov., 1918, p. 586.

eration show that there must be smaller bodies within the nucleus, each containing the potentialities of the entire organism. Ritter<sup>21b</sup> has recently insisted that the concept of *heredity* must be applied unreservedly to these one-celled organisms, many of which are quite complex in structure and undergo a true ontogeny. Indeed, the experimental studies of Jennings and his students have demonstrated the transmission of individual peculiarities, both of structure and function. As for the metazoa, despite the considerable evidence for chromosomal "individuality" and for the localization of genetic "factors," it seems to be entirely premature for us to assume the existence of a mosaic of parts, rigidly predetermined and incapable of making good a loss. One should recall what happened to an earlier "mosaic theory" of development.

To go to the other extreme, it might be supposed that for each form of organism there was at least one substance, or molecular structure, which was typical for it, and which determined its specific physical and chemical characteristics. The other constituents of the adult body would be modifications of this typical substance, which had lost certain of its original components or acquired new ones. This specific protoplasm would have some points in common with the "germ plasm" of Weismann. It might be credited with the power of indefinite growth and self-division, so long as these were not checked by counterbalancing forces. When completely checked, a growth equilibrium would be established which would represent the normal form of the species in question.

The rather vague and indefinite point of view here suggested would avoid, however, the tangle of unverified assumptions that are involved in the hypothesis of a "germ-plasm," conceived as an aggregation either of Weismannian "determinants" or twentieth-century "genes." The admitted possibility that certain material particles of the nucleus are functionally related to separately heritable adult characters does not constitute

<sup>21b</sup> The Unity of the Organism, Chapt. XII, XIII.

a proof that the entire organism develops through the combined activities of such particles. Moreover, even if such a complete germinal representation of adult characters were shown to exist, only a part—and a minor part—of our difficulties would be solved. We should still have to explain how the elementary parts of the body came to arrange themselves in proper spatial order and in proper chronological sequence during development. Blocks do not build themselves into houses. Driesch points out that historically vitalism and epigenesis have always been closely related, while the mechanistic school has commonly adopted some form of preformationism. Such a connection is far from being logically necessary, however. To me it would seem that preformation lent itself most readily to vitalism—to the notion of a builder who put the blocks together. In our particulate theories of organic differentiation, we commonly leave out of account the spatial and chronological relationships of the parts, or rather we take them for granted. We assume that somehow our "organismules" will find their way to their proper places at the proper moments, just as in a laboratory experiment the experimenter himself sees to it that everything is at each moment just where it belongs.

Let us return to an illustrative case, already considered, and ask why no one has ever seriously proposed a preformation theory of the earth's origin. Most moderns (M. Bergson is an exception) believe that our present world was the inevitable outcome of forces that were inherent in a fairly homogeneous molten mass, interacting with those of its cosmic environment. It has never been thought necessary to invoke the aid of special "determinants" to account for the various geographic and geologic features of our planet's structure. In dealing with inorganic things we are content to let our analysis rest, in the lack of more detailed information, with the acceptance of such general principles as "creative synthesis" or the "multiplication of effects." We simply

have to admit that differentiation means just this fact of *de novo* formation. Otherwise it means nothing at all.

We must, however, recognize certain essential differences between the development of a sea-urchin from an egg and that of our world from the structureless spore which was long ago liberated by its nebular parent. Let us suppose that some experimental cosmogonist, using the refined technique of a Morgan, Roux or Driesch, had skilfully removed about three quarters of our newly formed globe, leaving the remainder to reconstruct itself as best it could. The spherical shape would doubtless have been quickly restored, but is it likely that there would have formed in the ensuing ages just that same arrangement of Europe, Asia, Africa, America and the Islands of the Sea that we now find upon our maps? Unfortunately it is too late to perform this experiment, but I think that most geologists would expect a much modified world as the result. Indeed, if the excision had been made after the mixture of molten substances had begun to separate we should be perfectly certain that a quite "abnormal" world would have been the outcome. All this may be granted.

Let us ask another question. Why is it that no modern thinker<sup>22</sup> has set forth a preformation theory of *racial* evolution? It is only in accounting for individual development that this has been thought necessary. Yet the same paradox of *de novo* formation would seem to confront us in both cases, while other essential points of resemblance between phylogeny and ontogeny have often been pointed out.

One difference, doubtless, is that every process of phylogeny is regarded as a unique thing, while ontogeny is merely the *n*th reduplication of a known type, the character of which can be stated in advance. Hence it is that we are satisfied to resign the former process to the realm of "chance," while the latter we come to look on as determined in advance. Another difference seems to be that we look upon racial evolution as largely swayed by exter-

<sup>22</sup> We must except Bateson.

nal factors, of the haphazard sort which operate in the realms of geography and meteorology; while individual development appears to be swayed chiefly by internal factors, and to pursue its preordained course in a high degree independent of the outside world.

But where in all this is the necessity for preformation? That two specific types of protoplasm, under identical conditions of environment, will give rise to widely different organisms implies, of course, considerable difference in the protoplasms. It does not, however, compel us to believe in the existence of correspondingly numerous differences in the two cases. A single initial difference between two physico-chemical systems may determine a multitude of differences at the end. For example, the presence or absence of a certain amount of annual rainfall on a given area of the earth's surface would determine the nature of an indefinite number of other characteristics, both geographical and biological. We do not in this case endeavor to pick out a particular element of the cause to account for each particular element in the effect. Driesch's assumption that any "mechanical" (*i. e.*, non-vitalistic) conception of the developing organism must be based on a preformation of parts may once more be dismissed as untenable.

Some preformation there is to be sure. Recent Mendelian studies, particularly the investigations of sex determination, make it highly probable that certain adult characters, though perhaps in no case single anatomical structures, are represented by spatially separated particles in the nucleus. Furthermore, a certain amount of "promorphology" has been demonstrated in the cytoplasm of the unfertilized egg, though this is perhaps to be regarded as representing merely an early stage in individual development. I feel bound to express the belief, however, that many recent students of Mendelian inheritance have carried their factorial speculations far beyond the evidence, and that their detailed localization of representative particles may prove in the future to have more interest for psychology than for genetics. We

are dealing with a field in which ever more minute differences are being distinguished—many of them by purely subjective tests—and one in which the ratio of inference to observed fact is ever lengthening. May it not be that we have here hitherto unsuspected possibilities of self-deception on the part of even our most competent investigators? The subject is one which seems to me to deserve more attention than it has received.

On the whole, we are not compelled to assume the existence of any more preformation than can be experimentally demonstrated. And it may be regarded as settled that we have no parcelling out of "determinants" to appropriate cells during ontogeny, such as Weismann imagined. The "sex chromosomes," which seem to be the best authenticated instances of material bearers of hereditary traits, do not pass into definite body cells in the course of development and thus give rise to the primary and secondary organs of sex. Rather are they to be found distributed in every cell of the body. The assumption that they set free their characteristic determinants only in particular cells has no experimental or observational foundation.

Now, I am quite aware that any such "intra-selection" hypothesis of organic regulation as has here been advocated will be rejected by a large proportion of biologists on the ground that it is entirely superfluous. Various types of self-regulating mechanisms have been found in the non-living world, and the phenomena of growth and regeneration have long been known to be duplicated in crystals. Przibram has gone to considerable lengths in pointing out analogies between the behavior of the so-called "fluid crystals" and that of a regenerating organism.<sup>23</sup> And these analogies are reinforced by further ones, based upon the regeneration of crystals of hemoglobin. Many characteristically "vital" phenomena were

<sup>23</sup> (*Archiv für Entwicklungsmechanik*, October 16, 1906.) Likewise Torrey (*Scientific Monthly*, December, 1915) has discussed some interesting analogies between certain inorganic phenomena and the processes of "acclimatization" and "regulation."

observed by him in these studies, among which the most impressive was doubtless the making over of a softened hemoglobin crystal by a process of "morphallaxis," *i. e.*, the readjustment of the matter already contained in the fragment. There must thus be recognized in these non-living masses of matter a tendency toward the attainment of a specific form. And it seems plain that this tendency may realize itself in more than one way. Yet we should never, in this case, think of proposing any hypothesis of "trial and error," nor speak of the choice by the crystal of "means" to an "end."

Now, I will hasten to express my own belief that the phenomena in the two cases do not differ in any very fundamental way. *I am disposed to regard the regeneration of a crystal, the reconstruction of a mutilated organism, and the solving of a problem by a mathematician as members of a single series of increasing complexity. They have in common the reattainment of a condition of equilibrium which has been overthrown.* The fact that the organism is possessed of life, or that the mathematician has a conscious end in view do not alter the situation.

Such a "regulative" tendency in the inorganic world is recognized by physical chemists as the "principle of mobile equilibrium," or the "theorem of Le Chatelier." As stated by Lewis,<sup>23a</sup> this law asserts that "when a factor determining the equilibrium of the system is altered, the system tends to change in such a way as to oppose and partially annul the alteration in the factor. The same idea is conveyed by saying that every system in equilibrium is conservative, or tends to remain unchanged." Bancroft<sup>23b</sup> has given to this principle the dignity of a "universal law," pointing out analogies in the realms of biology, sociology and economics. More recently, its importance in ecology has been urged by Adams.<sup>23c</sup>

<sup>23a</sup> "A System of Physical Chemistry," Vol. II, 1916, pp. 140-141.

<sup>23b</sup> *Science*, Feb. 3, 1911.

<sup>23c</sup> AMERICAN NATURALIST, Oct.-Nov., 1918; Jan.-Feb., 1919.

In the regeneration of the more familiar type of crystal, the latter doubtless goes about its task "unhesitatingly," we may believe. But this is not true of every inorganic system. "In a stream [of water]," says Jennings, "opposing actions of all sorts are combatted in ways almost as varied as in organisms: a hole is filled up, a dam overflowed, an obstacle circumvented, another obstacle floated away, a bank of earth undermined or cut through; and the stream finally reaches the sea."<sup>24</sup> Must we not recognize important points of resemblance between such behavior and that of a penned-up cat, scratching wildly at the objects in its cage until finally a way out is found?

But if we admit this essential unity between the living and the non-living in respect to their method of correcting a disturbed equilibrium, why should we have resort in one case more than the other to a theory of "contingency" as regards the relation of means to end? Why may we not suppose the regulative processes of protoplasm to proceed as directly toward a goal as those of a crystal?

Answering the first question, I would say that the conception of contingency has been introduced into this discussion merely in the sense of a denial of teleology. Such a denial has been deemed necessary only in the case of organic phenomena. For inorganic events are seldom thought of as governed by "ends," and the question of "means" does not therefore arise. But in this respect there is really no difference between the living and the non-living.

The reason why the regulative processes of protoplasm probably do not proceed as directly toward a goal as those of a crystal lies, I believe, in the vastly greater complexity of the former. But it does not seem likely that any rigid distinction can be drawn. If it is really true that a damaged crystal of hemoglobin can restore its original form without the taking on of new material, it seems hardly likely that this rearrangement is effected

<sup>24</sup> *Johns Hopkins University Circular*, 1914, No. 10, p. 16.

by the simple transfer of material from one point to another along the straightest possible paths. There is doubtless much random molecular movement which serves only to retard the consummation of the process.

*The more complex the system with which we are dealing, the more of these "fortuitous" steps will intervene between overthrow and recovery of equilibrium. The chances that an entirely new disturbing factor will directly call forth the means to its own removal will correspondingly decrease. The more plainly, therefore, will the adjustment proceed in an "experimental" fashion.*<sup>25</sup> Processes which favor the restoration of equilibrium (*i. e.*, which satisfy the need) will be accelerated; those which work in a contrary direction will be retarded.

At this point it may be profitable to cite certain closely related utterances of Jennings:<sup>26</sup>

The condition which results in . . . regulative action is the presence, in a system, of a constant force, or stream of energy having a uniform tendency or direction (or set of such forces), together with intermittent forces having varied tendencies; whenever this condition exists, regulative action appears. . . . When the constant stream of energy is restrained for some time from producing its usual effects, it overflows in various directions, depending on the distribution of the resistance and amount and intensity of the free energy. It thus produces one effect after another. Often, at the end, one of these effects is of such a nature as to overcome or avoid the restraint; the stream of energy may then continue in the channel thus opened.

Has our prolonged discussion now led us, after all, merely to a denial of the scientific validity of the adaptation concept? I think not. The concept of adaptation stands upon the same footing as those of life, organization, function, food, enemy, offspring, environment, stimulus, heredity and the scores of other indubitable facts with which biology deals. By the use of pedantic circumlocutions, all of these various expressions could doubtless be avoided, and our ideas thus squared with the most rigid demands of "mechanistic" philosophy.

<sup>25</sup> Of course, such expressions as "experiment" and "trial and error" must be used in a strictly objective sense, so far as they are given any explanatory value.

<sup>26</sup> *Johns Hopkins University Circular*, 1914, No. 10.

But would such a renunciation bring us any nearer to the truth? Only if we are ready to regard the whole science of biology as a provisional one, a mere temporary resting place on the way to the more "exact" knowledge which constitutes mathematical physics. How many of us are prepared to make this admission?

Before passing on to the next subdivision of our field, a few words are desirable in answer to another general criticism which may be raised against the line of argument here followed. Exception may be taken to the apparent assumption that the responses to a new situation, whether physiological or psychological, are wholly random. Many responses are so obviously direct and unvarying as to appear "fatally" determined.<sup>27</sup>

Again, even where "experimentation" or "trial and error" is admittedly concerned in the process, the tentative efforts frequently lie within a quite restricted range of possible movements, and from the first approximate the goal to be reached much more nearly than if they were wholly undirected. Thus the experiments of Hobhouse<sup>28</sup> upon various mammals suggest to him "that recent writers have overestimated the effect of pure accident." Furthermore, he concludes that "the more a success was accidental the less likely were the animals to take advantage of it." So, too, in learning to throw at a mark, we do not commence by casting our missiles indifferently in every direction, but from the outset we throw them in the general direction of the target. And the same is palpably true when we attempt the solution of a mental problem. The trains of thought are doubtless "spontaneous," as pointed out above, but certain more or less relevant trains are favored in advance. It is from these that our selections are made.

Now, all these difficulties seem to me more apparent than real. After the first dawn of conscious experience, no situation is wholly new. Every problem which arises contains elements in common with earlier ones which we

<sup>27</sup> It is these which Loeb seems to regard as the more typical ones.

<sup>28</sup> "Mind in Evolution," 1915, pp. 236-237.

have already solved. This is the more true the more complex our problem. The "newness" of the latter may relate to a very few features, the residue consisting of elements which, in the last analysis, have been solved in an entirely empirical fashion. And the same may doubtless be said of those adaptive physiological responses which are generally assumed to be unconscious. As regards the fixed reactions known as "tropisms," I have already pointed out the probability that the predominantly adaptive character of these has been the outcome of racial history and therefore of some form of selection.

#### V. EVOLUTION AND "CONTINGENCY"

In the two preceding sections of this paper stress has been laid upon manifestations of the power of self-adaptation in the individual organism. Very little has been said regarding those fixed structural and functional mechanisms by which the more usual needs of life are provided for. The origin of such structures and functions—"adaptations," as they are familiarly called—must be accounted for in any adequate theory of evolution. Now, I have already argued that no theory of evolution, so far as it is scientific, can admit the possibility that the needs of the organism may call forth in any direct way the initiation of those processes by which these needs come to be satisfied. Let us look somewhat further into this question.

The field of organic evolution is one which has lent itself in a high degree to vitalistic and quasi-vitalistic exploitation. From the time of the establishment of the doctrine of descent, there were always persons who, in spirit, still clung to the creation principle, while accepting in form the newer ideas. Indeed, among biologists themselves, there have always been those who have seen in organic evolution the working out of a "perfecting principle," in a large degree independent of environment. Even Lamarck, who propounded one of the chief naturalistic accounts of this process, admitted that life

“tends by its very nature to a higher organization.”<sup>29</sup> The botanist Naegeli is one of the best known exponents of such a view. With some, like St. George Mivart, the question has been closely interwoven with special theological beliefs.

This writer believed in an “innate tendency to deviate at certain times and under certain conditions,” which tendency he held to be “an harmonious one, calculated to simultaneously adjust the various parts of the organism to their new relations.” And this guiding hand seems to have been exercised not only in the direction of satisfying the needs of the organism itself, but in adapting the latter to the needs of man. Speaking of the evolution of the horse, he tells us :

The series is an admirable example of successive modification in one special direction along one beneficial line, and the teleologist must here be allowed to consider that one motive of this modification (among probably an indefinite number of motives inconceivable to us) was the relationship in which the horse was to stand to the human inhabitants of this planet.<sup>30</sup>

Others, like Wallace, have had recourse to such a guiding principle only in accounting for the origin of man.

In recent years, the philosopher Bergson has adopted a vitalistic theory of evolution, weaving it into a metaphysical system of which an important feature is the essentially creative character of time or “duration.” We see the world of living things moving grandly on through the ages, impelled by a mysterious force, the “*élan vital*,” and flowering out spontaneously into a never-ending succession of living wonders. Such a conception may stir the imagination, but it does not add to our knowledge.

Now, curiously enough, this “teleological” factor has been introduced by various writers to explain two exactly opposite classes of cases : (1) the origin of adaptive char-

<sup>29</sup> *Philosophie Zoologique* (Elliot’s translation), p. 239, and elsewhere. Lamarek’s statements are not wholly consistent, however, and I cannot feel quite sure that he had in view any principle distinct from the one with which his name is commonly associated.

<sup>30</sup> “*Genesis of Species*,” p. 151.

acters (Paley's argument), and (2) the origin of highly perfected structures and functions which are not believed to be adaptive in the biological sense, at least to the extent of influencing survival. The musical and artistic faculties of man belong to this second class.

Natural selection, as is well known, provides us with at least a formal explanation of the first class of characters, but not of the second. Lamarckism, with a varying degree of plausibility, accounts for the origin of characters belonging to either class. That both of these theories are, in last analysis, theories of selection has been pointed out in section II.

But the claim is to-day heard on various sides that both natural selection and Lamarckism have broken down completely, and that no other existing evolutionary theories merit serious attention. So impossible is it for some biologists to square the widespread appearance of adaptation in nature with their own special theories of life that they seek to escape the dilemma by declaring this appearance to be largely illusory. Thus Loeb<sup>31</sup> tells us:

While it is possible for forms with moderate disharmonies to survive, those with gross disharmonies can not exist and we are not reminded of their possible existence. As a consequence the cases of apparent adaptation prevail in nature.

In much the same vein, Davenport<sup>32</sup> writes:

Strictly, we may say adaptation is not the thing that is brought about, but rather absence of non-adaptedness. Such adjustment as we find is, doubtless, only such a residuum of variants as has not proved incompatible with conditions of existence.

One might profitably compare such conclusions as the foregoing with the findings of Cannon,<sup>33</sup> based upon the detailed study of certain adaptive mechanisms in man. To most of us the conviction is doubtless irresistible, not that such mechanisms now exist because of their *harmlessness*, but that they came into existence, step by step, *on account of their utility*.

<sup>31</sup> "The Organism as a Whole," p. 344.

<sup>32</sup> AMERICAN NATURALIST, August, 1916.

<sup>33</sup> "Bodily Changes in Pain, Hunger, Fear and Rage," 1916.

Taking heart from this skepticism among the biologists themselves, reactionaries are boldly coming forward with the assertion that the evolution principle has been discredited. It is certain that the spread of such ideas is not calculated to further the advancement of knowledge. Lack of an adequate hypothesis is not disproof of any possible hypothesis.

Moreover, it would now seem that some of these admissions of inadequacy have been premature. Much of the recent abandonment of the natural selection theory has been due to neo-Mendelian dogmatism. Selection, it is claimed, can only separate strains having different mean characters. It can not change the mean characters of a pure strain. But the experiments of Castle and some other breeders may be cited as evidence that such a contention is far from being established. And even those who reject Castle's interpretation of these results have been forced to concede that in some cases selection may bring about the indefinite modification of our stock —call the process "sorting" if we will.

So, too, the Lamarckian principle occupies the curious position of being dogmatically denied or wholly ignored by a large and influential class of writers, at the same time that others are able to adduce apparently convincing arguments for its reality. We certainly have a vast array of indirect or circumstantial evidence for this principle, derived from an inspection of the actual products of evolution as we find them. And we have a certain amount of direct, experimental evidence which can not be thrown aside as irrelevant or untrustworthy. While, therefore, sweeping conclusions regarding the Lamarckian factor are doubtless premature, the dogmatic denial of this factor very nearly amounts to self-stultification.

Thus, if we may read the signs of the times, the two chief naturalistic explanations of evolution may survive the fire of destructive criticism and again play an important part in our interpretation of life. By this, I do not wish to be understood as arguing that either or both of these theories constitute an adequate explanation (even

in the sense of a description) of how evolution has come to pass. For many years past, I have been endeavoring to weigh the evidence for and against both of these hypotheses and I have reached the same verdict with respect to the two: *each is both proved and disproved*. It is not that adequate evidence is lacking, as some assume. Rather, in each case, is the evidence well-nigh overwhelming—*on both sides*.

Now, obviously, no single proposition can be both true and untrue at the same time. What is meant here is this. I believe the selection of virtually continuous variations and the inheritance of functional and environmental modifications to have both played *some* part in evolution. And I do not hesitate to say that the evidence in favor of such a view is of the same general character as the evidence for the evolution theory itself, and nearly as convincing.

On the other hand, it seems no less probable that the operation of each of these factors is strictly limited. Indeed, it would appear likely that much of the adaptiveness in nature is not adequately accounted for by either process or by both taken together. There may well be other factors the existence of which is as little suspected to-day as was that of natural selection before the time of Darwin and Wallace.

But will our explanations remain purely naturalistic, or will they find room for extra-natural directive agents, by whatever name called? Will they, like the two chief historic theories, base themselves on the contingency of every adaptive variation in structure or function, antecedent to the test of experience, or will they be forced to concede a primary adaptiveness inherent in living matter.

Many of those who admit the widespread occurrence of natural selection as a process, are wont to deny to it any *explanatory* value. To quote a now familiar saying, it is said that the survival of the fittest does not account for the origin of fitness. The real cause of modification, these writers insist, is to be sought in the process by

which variations are produced and not in the fact that many of these variations fail to maintain themselves.

This argument is so plausible that it seems self-evident. And indeed in a sense it is. But there is another sense in which it is quite specious. Truly enough, no individual can survive which is not first born or hatched, or in some way brought into being by its parents. And those peculiarities which distinguish one individual from another are largely ushered into life along with it. They exist prior to selection. But fitness is a *relation*, not an absolute property of the organism. The word denotes merely a certain measure of adjustment to specific conditions of life, and the degree of this adjustment we know to vary almost indefinitely. To say that the conditions of life, acting through the selective process, can not be the cause of an increasing degree of fitness is like denying that a sculptor produces a statue, on the ground that he does not create the stone. It is well to note that even the sculptor's function is wholly selective. He eliminates certain portions of an unshaped mass of material.<sup>34</sup>

The foregoing analogy admittedly fails in one important respect. It implies that the possibilities of selection in a given race are wholly unlimited. We know this to be very wide of the truth. The question to be answered here is merely whether or not they are completely *random* in the sense which has been employed throughout this article.

Now, some selectionists are wont to deny the completely random character of variation. So far as this is simply a denial of the infinite variability of any species, it is a mere truism. We may perhaps admit the possibility that a given strain might, through rigid selection, acquire the "habit" of varying preponderantly in certain definite directions, thus limiting the possibilities of further evolution within that group. And we might even grant that such definitely directed variations might ac-

<sup>34</sup> I do not recall the previous use of this analogy, but it is such an obvious one that it has doubtless occurred to many.

cumulate without the influence of selection at all (orthogenesis). But can we, without departing from naturalistic grounds, conceive of the production in this way of a structure in anticipation of a need? May we even conceive how appropriate variations could be called forth by an already existing need.

Of course, much obscurity of thought may be concealed beneath this innocent-looking word "need." What is a need? It is notorious that what is a luxury to some of us is a necessity to others. Our needs grow with our incomes. And this line of reasoning is directly applicable to sub-human realms. What an animal has, if this adjusts it to certain conditions of the environment, may be regarded retrospectively as the fulfilment of a need. Thus eyes fulfil the need of seeing. But can we say that such a need existed before the appearance of visual organs? There are beyond doubt still many forms of wave-motion or molecular vibration for which we have no organs of perception. Thus, in a large measure the organism creates its own needs, even in an unchanging environment. The word "need," like the word "end," is one which has a distinctly teleological implication. The more factors of the environmental complex an organism is brought into relation with, the better is it adjusted to its life conditions, and—other things equal—the higher position it holds in the scale of life. But these adjustments are only thought of as satisfying needs when we come to look back on what has actually happened.<sup>35</sup>

There is a more limited sense, however, in which the use of this expression involves us in no such obscurities. All those fundamental requirements, such as food, oxygen, protection from enemies, etc., may be termed *needs*, without there resulting any confusion of thought. Now, anything which led to the removal of one or more of these fundamental requirements—say the drying up of a lake—might bring about the extermination of an entire species, unless some adaptive response were made.

<sup>35</sup> They may all, however, be properly termed *adaptations*, as has already been said.

Here, likewise, we may legitimately speak of the *need* for some sort of readjustment. Let us, then, restrict the word to anything without which a species would become extinct.

With this limitation of meaning understood, let us return to certain questions which I have left unanswered. Can we, on naturalistic grounds, conceive how an appropriate trend of variation could anticipate a given need; or can we even conceive how it could be called forth by an existing need? The former possibility certainly can not be admitted without frankly taking refuge in principles which lie beyond the range of scientific analysis. The latter possibility has, however, been vaguely implied by some writers on evolution.

So far as the "need" might be the result of some marked change in the environment or in the functional activities of the organism, it is credible that new variations might be offered to selection as a consequence of disturbances in the germinal material. But how could these occur preponderatingly in the direction of meeting the particular need in question? *Only in one way, so far as I can see, and that way is by the previous adaptive modification of the parent body.* For the latter may adapt itself experimentally, according to principles already discussed. The germ-cells could not adapt themselves experimentally, since the need is commonly one which does not as such affect them at all. Thus, the imperative demand for *directed* germinal variations—or at least ones of a useful sort—can be met, so far as now appears, only by assuming the transmission to the germ-cell of adaptive responses of the parent body.

The Lamarckian principle has the added advantage of being able to account for many of the "luxuries" of organization—adaptations, in the sense of fitting their possessors for a fuller and more varied life, but not of any conceivable survival value. Our own race, as has often been pointed out, is endowed with multitudes of such faculties. But we are sadly in need of direct experimental evidence along these lines.

Biologists of the future may recognize the importance of determining experimentally whether the germinal variations of a species ever respond to changed life conditions in such a way as to shift the mode of any character in the direction of greater adaptation. If such a general tendency as this were revealed, and if, at the same time, the transmission of somatic modifications were rigidly excluded, we should be brought to a crisis in the history of our science. The question at issue would not be merely the adequacy or this or that hypothesis. It would be the adequacy of our recognized scientific methods to deal with such problems. Despite the lengthy arguments with which I have sought to defend a purely naturalistic position, I should not, in advance, be supremely confident as to the outcome of such experiments. It might, after all, turn out that there was just such an "immanent teleology" in living things as the vitalists claim. If this should prove to be true, science would have to re-survey its territory and set itself new boundaries well within the old ones.

Such an undertaking, like that of settling once for all the "acquired characters" question, would doubtless be beset by great technical difficulties. But these difficulties should not be insuperable. So long, however, as "genetics" is held to be nearly or quite synonymous with Mendelism, evolution along dynamic lines is likely to languish. We must grant the enormous strides which have been made in our knowledge of the inheritance of certain types of variations, but the much more fundamental question of the causes of these variations is almost as far from solution as in the days of Darwin.

In conclusion, I would say a few further words in regard to my use of the expressions "contingency" and "chance" throughout these pages. It is needless to say that I have not used these words as synonymous with uncaused. I have spoken of an event as contingent, merely in the sense of its being causally unrelated to something else: for example, a variation in relation to a need to be fulfilled. Whether or not, in the last analysis, all things

are causally related in an Absolute, or whether the Universe is pluralistic in its nature, need not concern us here. That there may be some measure of pre-established harmony among its various parts is possible. It has recently been ably argued—and by a chemist, not a theologian—that there exists such a pre-established harmony between the organic and the inorganic worlds as a whole.<sup>36</sup>

But even granting such very problematic relationships as this, we can not deny that much happens in a purely "accidental" way. No degree of fitness on the part of the environment for life in general can avail to prevent the wholesale destruction of organisms which "happen" into unfavorable surroundings. That all of the special adjustments between organism and environment arose primarily through contingency or chance in the sense here indicated is the main thesis which I have defended in these pages. There may be little of an original nature, either in the views proposed or the arguments used in support of them. But I believe that this essay may serve a useful purpose in bringing together a number of apparently distinct problems under a common viewpoint.

<sup>36</sup> L. J. Henderson: "The Fitness of the Environment" (1913), "The Order of Nature" (1917).